

Nymphs of the Formosan Subterranean Termite (Isoptera: Rhinotermitidae): Aspects of Formation and Transformation

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ABSTRACT Mature colonies of the Formosan subterranean termite, *Coptotermes formosanus* Shiraki, like most other termite species, produce a reproductive caste in the form of nymphs that subsequently give rise to alates. Temporal production of nymphs in *C. formosanus* was monitored in monthly collections from four field traps in New Orleans, LA. Nymphs were present throughout the year with peak numbers observed during October/November and May. Large nymphs first occurred in December and peaked in March. Fewer than 1.5% workers formed nymphs within 3 months after collection from the field and after removal of the preexisting nymphs. Collections from other colonies, kept in the laboratory for >2 yr, did not produce any nymphs. It is speculated that a nymph induction factor (NIF), possibly coming from a mature physogastric queen, elicits nymph formation. The same or a similar factor may also be responsible for further development of nymphs and their transformation to alates. In the absence of this latter factor, the nymphs, except those in the most advanced stage of development, are either cannibalized or transform into brachypteroid neotenics. A scheme for the formation and transformation of various developmental stages within each caste of *C. formosanus* is presented.

KEY WORDS Formosan subterranean termite, *Coptotermes formosanus*, nymphs

A TYPICAL TERMITE COLONY possesses a number of different castes and developmental stages within each caste (Miller 1969, Thorne 1997, Roisin 2000). One such caste, often present in mature colonies, is the brachypterous nymph or just nymph. The nymphs have wing buds and through a series of molts give rise to the winged adults or alates. Therefore, in this polymorphic society, nymphs are considered the reproductive caste, and the rest of the basic forms such as workers and soldiers are nonreproductive castes. The Formosan subterranean termite, *Coptotermes formosanus* Shiraki, introduced into the continental United States around the middle of the last century, has become a serious pest of houses and live trees in several southern states and in Hawaii. *C. formosanus* colonies are very large with several million individuals present in a mature colony (King 1971). In Louisiana, *C. formosanus* produces huge swarms of alates from late April to mid-June (Henderson 1996). Swarming in this species, as in all other termites, is the primary mechanism for dispersal. Su and Scheffrahn (1987) reported that one caged colony of *C. formosanus* in Florida

released 68,729 alates in a 5-d period and 26,500 flew from the nest on a single day.

Whereas there is considerable literature on soldier formation, very little is known, and most of it speculative, about the formation of nymphs. Lüscher (1962) suggested that caste formation was regulated by factors that operate at three levels: environmental, acting on the whole colony; social (pheromones) acting among the individuals; and individual (hormones), which act within the individual. Based on measurements of brains in newly hatched larvae of *Reticulitermes flavipes* (Kollar), Thompson (1917) reported the presence of two types of larvae: the reproductive type with large brains and worker-soldier type with small brains. This was later refuted by Hare (1934). Buchli (1958) suggested that it is the physiology of the whole colony that determines the destiny of the individual. In *Kaloterms flavicollis* F., Lüscher (1961) reported that in the presence of abundant food, juvenile hormone production is reduced, which leads to alate production. Lüscher (1973) also hypothesized that in lower termites occurrence of nymphs may be inhibited by the presence of primary reproductives. Contrary to his earlier report, Lüscher (1976) suggested that pheromones, rather than larval nutrition, played a key role as exogenous regulators of developmental pathways. In *Zootermopsis nevadensis* Hagen, it was reported that the onset of alate development is

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determined by the ratio of nutrient-gathering castes to nutrient-receiving castes in the colony (Hahn 1993).

In contrast to the dearth of literature dealing with the initial formation of nymphs, literature on their transformation, particularly into secondary reproductives or neotenics, is fairly abundant (reviewed in Myles 1999). Lüscher (1961) suggested that orphaning is the main factor that provokes formation of replacement or secondary reproductives. Similarly, in the Australian species *Coptotermes lacteus* (Froggatt), many neotenics were formed after a colony was orphaned (Lenz et al. 1988). In *Reticulitermes hesperus* Banks, Pickens (1932) suggested that an inhibiting secretion, produced by a queen, prevented the development of other reproductives in the colony. Lenz and Barrett (1982) suggested that in *C. lacteus* the development of neotenics may be regulated in two ways: 1) existing reproductives may inhibit the differentiation of a late stage reproductive nymph, or 2) they may prevent the sexual maturation of the resulting neotenics. In the neotropical termite, *Armitermes euamignathus* Silvestri, Costa-Leonardo et al. (1996) suggested that the development of nymphoids or brachypteroid neotenics seemed to be induced by the removal of queen inhibition. However, the glandular source and nature of this secretion/pheromone remains a mystery. Aside from the exogenous and endogenous determinants, Myles and Chang (1984) suggested that the actual differentiation process of (brachypteroid) neotenics results from a partial expression of the alate developmental program rather than a unique program. Among three species of *Reticulitermes*, it was reported that secondary reproductives were formed within 3 to 4 mo after separation of workers from the founding colony (Pawson and Gold 1996).

The present investigation was designed to study the temporal pattern of nymph formation and their subsequent transformation to alates or neotenics in *C. formosanus* with discussion of possible factors that regulate the development of these castes.

Materials and Methods

Collection Sites and Sample Collection. Four collection sites, three in the University of New Orleans (UNO) campus and one in New Orleans City Park (CP), in New Orleans, LA, were selected. Bucket traps (Su and Scheffrahn 1986) had been in place at these locations since 1999. Based on initial trap catch data and the presence of nymphs, four of these traps, one at each location, were earmarked for this study. Wood along with the termites in each trap was collected once a month for 1 yr. The infested wood was brought into the laboratory, and the termites carefully sorted into various castes and counted. The nymphs were removed, and the workers and soldiers were placed into transparent plastic boxes (17 by 12 by 6 cm) with fresh moist spruce wood pieces. These boxes were in turn placed in a larger box with a layer of water to maintain high relative humidity and kept under laboratory conditions. Based on visual rating, the nymphs were cat-

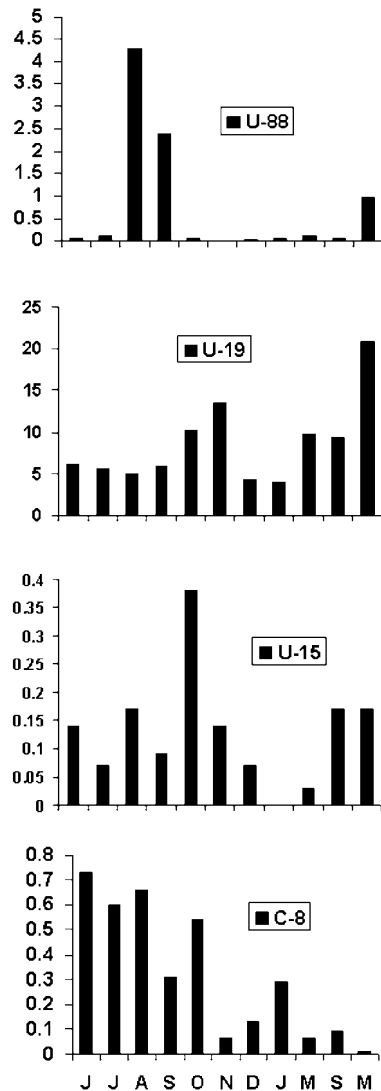


Fig. 1. Nymphs as a percentage of total trap collection of *C. formosanus* from four traps over a period of 12 mo. There were no termites in February.

egorized into small (very small wing buds, not extending beyond the first abdominal segment), medium (wing buds extending not beyond the third abdominal tergite), and large (wing buds extending beyond the third tergite and large body size). After sorting the nymphs from each trap collection, these together with workers and soldiers (in a proportion of 2:20:1) from their respective colonies, were placed in plastic containers with spruce wood pieces and kept in an environmental chamber maintained at $28 \pm 1^\circ\text{C}$, $\geq 80\%$ RH, and constant darkness. The remaining workers and soldiers were returned to their original containers.

In addition, termite collections, ranging in size from 5,000 to 10,000 workers and soldiers, from traps other than the previously listed were kept in an incubator at the above-mentioned conditions. Portions of termite-

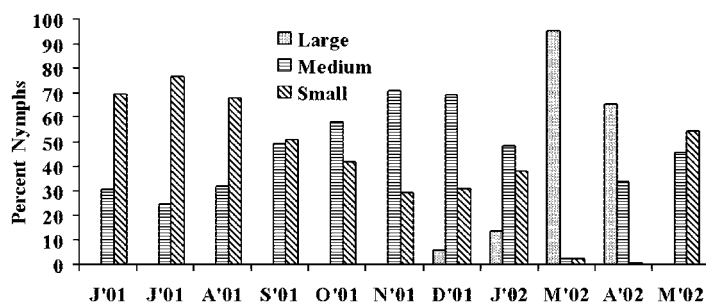


Fig. 2. Occurrence of small, medium and large nymphs of *C. formosanus* from trap U-19 over a period of 12 mo.

infested landscape ties and garden posts, containing preflight alates in addition to few workers and soldiers, were collected from the UNO area from late March to early April. These were kept in large plastic containers in the laboratory.

Observations. Each collection of workers and soldiers from each location (from which nymphs, if present, had been removed) was examined every 3 mo over a period of 1 yr for any new nymph that may have formed during the intervening period. When found, such nymphs were removed and categorized by size of the wing bud and number of antennal segments. Thus, nymphs with very small wing buds indicated their de novo formation rather than having been missed during the previous observations. Additional collections of 5,000–10,000 workers were routinely examined for nymph formation over an extended period of 2 yr. We also examined 115 nymphs of different sizes for head capsule width, number of antennal segments, presence of flagellates in the gut, and the status of their reproductive organs. A correlation coefficient between head capsule width and antennal segments was determined. Nymphs removed from the monthly collections of the four field traps were also examined at regular intervals to determine their growth and transformation into either alates or secondary neotenic. The last step in the transformation of nymphs to alates was closely monitored for the sequence of changes. Large nymphs, collected during March and April, were used for this purpose.

Results

Field Collections. All four traps yielded nymphs almost throughout the 12-mo observation period (Fig. 1), except in February, when it was too cold and the traps had very few or no termites in them. The highest incidence of nymphs in field traps, ranging from 4 to 21%, occurred in trap U-19. Total trap catches ranged from 431 in January to over 46,000 in April. Termite activity was generally very low from January to March. Among the other three traps, nymphal populations were significantly lower, ranging from 0 to 4.3% at any given time during the 12-mo observation. The U-19 trap showed two peaks of nymphs, one in October–November and a second in May. Traps U-88 and U-15 showed a similar trend, although the timing of the first peak was somewhat different from that of U-19. The

second peak in all these cases was coincident with the onset of swarming season. The C-8 trap (City Park), like U-88, had overall low numbers of nymphs collected, and there was no peak in May. Significant numbers of small, newly formed nymphs first occurred in May. Although a similar trend was observed in all four traps, data are shown only for nymphs from U-19 (Fig. 2). In July, >76% of the nymphs were small. Large nymphs started occurring in December and peaked in March, approximately a month before the start of the swarming season.

Nymph Formation. Although similar observations were made on all four trap collections, data are presented only for U-19 (Table 1). Once the existing nymphs were removed at the time of collection from the field, very few if any additional nymphs were produced under laboratory conditions. Three months after collection, the highest number of nymphs was produced in the November and May collections, coincident with original nymphal peaks. At 6 mo, the incidence of de novo nymph formation was extremely low and, almost no additional nymphs were formed during the next 6 mo. For the other three trap collections, the incidence of new nymph formation was negligible during the observation period. In addition, we did not notice any nymph formation in termite collections comprising 5,000–10,000 workers and soldiers that were maintained in the laboratory for up to 2 yr.

Examination of the large number of newly formed nymphs (all with very small wing buds) from the May collection revealed that these had 12–15 antennal segments (Fig. 3). It is speculated that these nymphs were derived from workers with 11–14 antennal segments, respectively, possibly after undergoing a molt. In rare cases, we found newly formed nymphs with 16 or 17 antennal segments. Head capsule width and antennal segment count were positively correlated ($r = 0.87$, $P < 0.0001$, $n = 115$). Very small ovaries and testes were for the first time observed in nymphs with 14 antennal segments. Apart from observing the actual molting process in several nymphs, guts of suspected newly molted nymphs were found to be devoid of all flagellates, an indication of a molt in workers.

Based on observations of nymphs freshly collected from field traps each month, it was evident that in mature colonies the new nymphs underwent a rapid development during the summer until most of them

Table 1. Occurrence of nymphs in field trap (U-19) collections of *C. formosanus* and subsequent de novo nymph formation under laboratory conditions

Collection month	Present at collection time (total termites)	% nymphs			
		Formed after (mo)			
		3	6	9	12
June 2001	6.20 (5428)	0.66	0.67	0.08	0.04
July	5.62 (5231)	0.01	0.02	0.00	0.00
Aug.	5.03 (7574)	0.01	0.01	0.00	0.00
Sept.	5.97 (5812)	0.24	0.00	Dead	
Oct.	10.16 (2756)	0.05	0.00	0.00	0.00
Nov.	13.55 (1904)	1.00	0.08	0.06	0.03
Dec.	4.32 (4652)	0.34	0.06	0.02	0.00
January 2002	4.04 (5272)	0.19	0.19	0.03	0.00
March	9.74 (431)	0.29	Dead		
April	9.36 (46356)	0.21	0.16	0.06	0.03
May	20.89 (2733)	1.44	0.28	0.11	0.09

All nymphs were removed at the time of initial examination.

were N-4 and N-5 stage (15–17 antennal segments). This was followed by a period of slow growth until December. After that, the nymphs became very plump. By early April, the freshly collected nymphs had undergone another molt, the antennal segments had increased to 18 to 19, and the eyes had bulged and later turned red. The wing buds also developed a light orange color at their bases (Fig. 4A). These seventh, and final, instars subsequently molted to alates.

Transformation of Nymphs. The large nymphs with orange wing buds underwent a last molt to become alates with 19–21 antennal segments (Fig. 4B). The wings quickly expanded, and the cuticle underwent complete melanization within 48 h. Examination of the infested logs containing preflight alates indicated that alates do not swarm immediately after melanization but remain in their nests and fly out in response to

specific weather cues as noted previously by Nutting (1969). First swarms, relatively small, were observed toward the end of April followed by large swarms during mid-May. Based on antennal segment data, it is speculated that the small number of nymphs formed after September, particularly those formed from smaller workers, may not become alates during the coming swarming season but remain nymphs for over a full year. The small nymphs collected from the traps and maintained in the laboratory with workers of the same colony did not grow much even after 2 yr and evidently died or were gradually cannibalized. The medium-sized nymphs, with 15–17 antennal segments, often transformed into brachypteroid neotenics (Fig. 4C), with rapid growth of their reproductive systems. Although the neotenics were fully melanized, they were never as dark as the alates and their wing buds

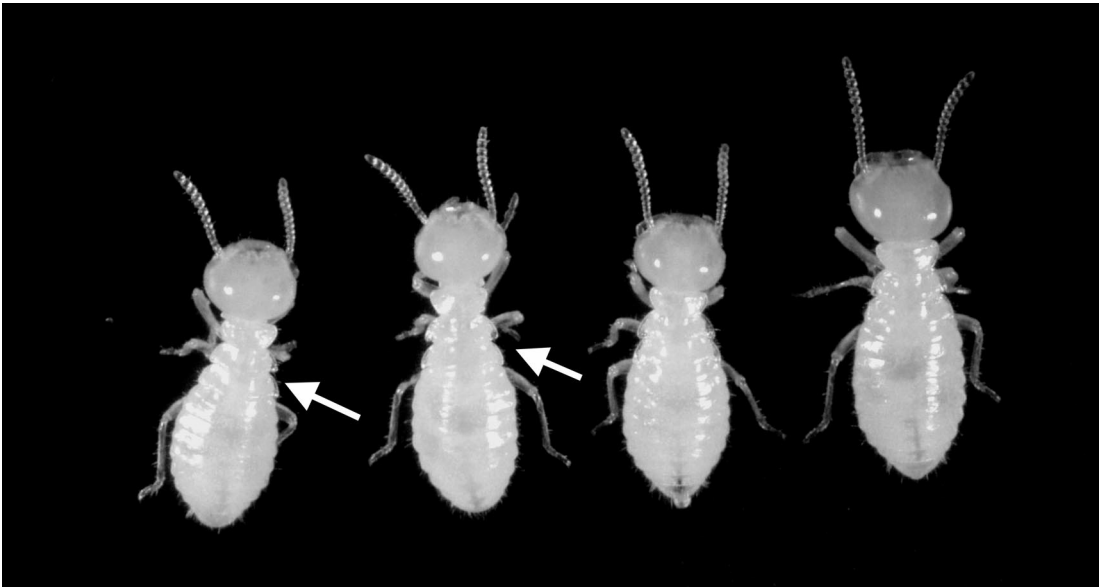


Fig. 3. Newly formed nymphs of *C. formosanus* collected during May. The nymphs from left to right have 12–15 antennal segments. Arrows indicate the very small wing buds.

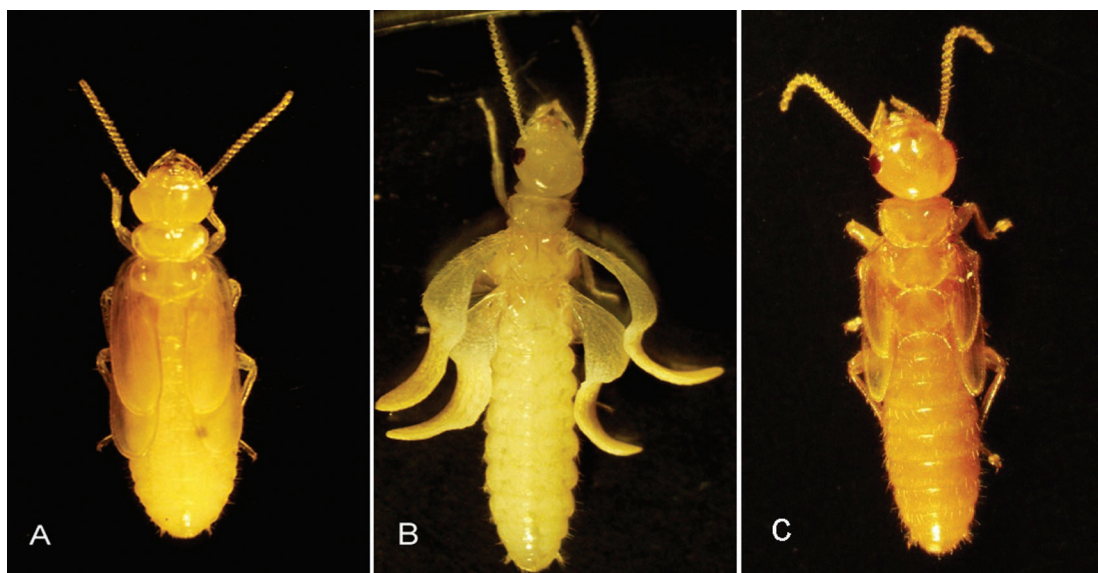


Fig. 4. Various stages in the transformation of nymphs of *C. formosanus*. (A) Final or seventh instar with bulged eyes and orange colored wings. (B) Newly molted alate, the wings are not yet expanded and the cuticle not melanized. (C) Brachypteroid neotenic male with dark red eyes and melanized cuticle. The neotenic has also fully developed reproductive system.

did not grow any further. Only the last instars, particularly those collected from the field during March and April, transformed into alates in the laboratory. During several years of observations on many thousands of workers, we found only a single case of an ergatoid neotenic, a reproductive form produced directly from the workers.

Discussion

Termite biology is so diverse, even among representatives within the same family (Parmentier and Roisin 2003), that robust generalizations are not often possible. Therefore, the data reported here seem applicable to *C. formosanus* specifically. Our observations indicated that only a few field collections of *C. formosanus* had nymphs. Apparently, the colony represented by the U-19 trap is a very mature colony producing large number of nymphs and alates (alate data not presented). There was a fairly good correlation between the events: small nymphs occurred in field collections when the existing nymphs had transformed into alates, and these in turn had swarmed. The workers could now divert their attention to this new crop of nymphs, feeding and grooming them during the molting process. It has been suggested that only mature colonies of *C. formosanus* produce alate swarms. According to Bess (1970), alates did not develop in 1-5-yr-old laboratory colonies. The observation that no nymphs were formed in younger colonies together with the fact that no nymphs ever developed among field-collected termites maintained in the laboratory for up to 2 yr suggests the involvement of a NIF, possibly originating from a mature or physogastric queen. Earlier studies of a number of species of

termites led to the speculation that an inhibitory substance produced by primary reproductives, especially the queen, prevented the formation of additional members of the reproductive caste (Pickens 1932, Wigglesworth 1961, Lüscher 1973, Bordereau 1975). However, no such pheromone/hormone has yet been identified. Our assumption of the presence of a NIF is supported by Darlington (1985) working on *Macrotermes michaelsoni* (Sjöstedt). She reported that removal of primary reproductives from 79 nests resulted in no more nymphs occurring in these colonies.

Antennal segment count in termites has generally been considered a good criterion of growth and molting (Buchli 1958, King 1971, Myles and Chang 1984). An examination of the newly formed nymphs with very small wing buds revealed 12-15 antennal segments. It is presumed that they arose from first to fourth instar workers with 11-14 antennal segments. We consider the first two instars after hatching from eggs as larvae, distinguishing these from workers in that they lack functional mandibles, require to be fed, and are unable to transform into presoldiers or nymphs. Buchli (1956a,b, 1958) reported that in *Reticulitermes lucifugus* Rossi the first two instars are undifferentiated and do not feed by themselves and that after stage 3 in large colonies, they may become either workers or nymphs. However, in *C. lacteus*, it was reported that after the first two instars, development forks into an apterous line and a nymphal line (Roisin and Lenz 1999). They further stated that the nymphal line comprises six instars followed by the alates in laboratory-reared colonies. It was only after August that we observed newly formed nymphs with 16 to 17 antennal segments, possibly arising from fifth instar or older workers with 15 to 16 antennal seg-

ments. Our observations suggest that the small nymphs, under field conditions, undergo rapid growth and molting until most of them reach medium size in ≈ 4 mo.

Large nymphs, with wing buds extending to the middle of the abdomen and bodies full of fat, first occurred in field trap collections around December. It was only the large nymphs collected after late March that molted into alates under laboratory conditions. The small nymphs, like those collected during July, never grew to the large stage in the laboratory. Also, both medium and large nymphs collected before March did not transform into alates. Whereas some of these were cannibalized by workers and soldiers (based on gradual reduction in their numbers and the fact that we did not observe any regressive molts), others transformed into brachypteroid neotenics or secondary reproductives. The transformation was evident with the development of dark eyes, melanization of body, retention of short wing buds, and rapid development of reproductive systems. The *de novo* formation of such brachypteroid neotenics (in the absence of preexisting nymphs) has been observed to be extremely rare in laboratory cultures of *C. formosanus*. Even rarer was the formation of ergatoid neotenic or third form reproductive, with only one found among dozens of colonies kept under observation during the past 4 yr.

Our observations indicate that the presence and continued delivery of a speculated NIF may be important to mediate the transformation of workers into nymphs and subsequently to alate stage. Because nymph formation in *C. formosanus* occurs only in large mature colonies, the overall population density of a colony may be an additional trigger. If the source of the factor is removed before the nymphs reach a critical point toward alate formation, such nymphs instead transform into neotenics. In this respect, *C. formosanus* is very different from many of the other lower termites. Becker (1969) reported that the genus *Coptotermes* seldom or never produce replacement reproductives. However, according to Myles (1999) nymphoids (brachypteroid neotenics) are common in some *Coptotermes* species. According to Lenz and Barrett (1982), the incidence of neotenics in field colonies of *Coptotermes* seems to vary greatly among species. In *Coptotermes acinaciformis acinaciformis* (Froggott), a species native to Australia, the incidence of neotenics is rare, whereas it is more common in New Zealand, where this species was introduced (Lenz et al. 1986). In studies of three species of *Reticulitermes*, Pawson and Gold (1996) observed that 75–100 workers kept by themselves for 3–4 mo developed supplementary reproductives. However, the possible presence of an inhibiting pheromone, as suggested by Lüscher (1961), does not explain why workers of *C. formosanus* removed from the colony do not transform into nymphs. Lenz et al. (1988) reported that many neotenics were formed after a colony of *C. lacteus* was orphaned. However, they did not state whether the colony had preexisting nymphs when it was orphaned. Later, Lenz and Runko (1993) re-

ported that experimental orphaning of *C. lacteus* field colonies in southeastern Australia resulted in production of 1–27 nymphoid neotenics. Either these colonies were mature and were already producing nymphs, or *C. lacteus* is very different from *C. formosanus* in this respect. Unlike brachypteroid neotenics, ergatoid neotenics arise directly from workers. In *A. euamignathus*, ergatoids occurred when nymphs were not available (Costa-Leonardo et al. 1998). Whereas the formation of ergatoids is very common in many species of termites (Myles 1999), it is very rare in *C. formosanus*.

The developmental scheme for various castes, including the formation and transformation of brachypterous nymphs in *C. formosanus*, is presented in Fig. 5. The eggs hatch into the first instars with nine antennal segments that molt to second instars with 10 antennal segments. The larvae do not feed by themselves. The second instars molt into workers having 11 antennal segments, functional mandibles, and a full complement of gut flagellates. Through a series of additional molts, the workers grow bigger and have up to 15 antennal segments. Any of these worker instars can molt into presoldiers that become soldiers through another molt. Occasionally, in mature colonies collected from the field, a sixth worker stage with 16 antennal segments was also observed. Based on antennal segment numbers observed in workers and nymphs, any of the worker stages can form nymphs, possibly in response to the nymph induction factor presumably coming from the mature queen. We base this on the observation that nymphs are routinely collected from field colonies but only rarely, if ever, in laboratory-held collections where there is no such queen present. Generally, each instar has one more

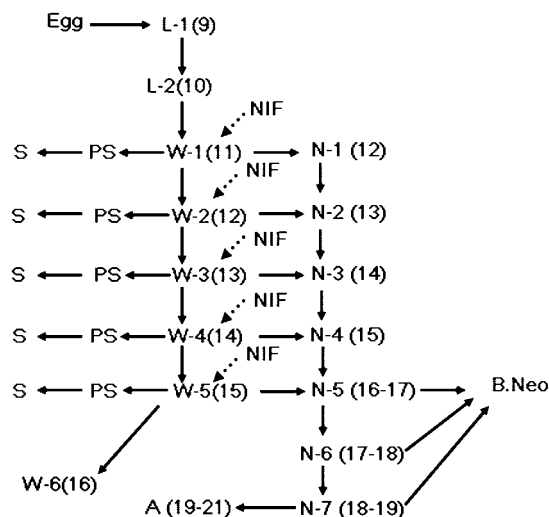


Fig. 5. Proposed flow diagram showing the development and formation of various castes in *C. formosanus*. The involvement of NIF is speculative (dotted arrows). (A) Alate. (B) Neo, brachypteroid neotenic. L, larva; N, nymph; PS, presoldier; S, soldier; W, worker. Numbers in parentheses indicate the number of antennal segments.

antennal segment than the corresponding worker from which it arose. In another rhinotermitid, *Schedorhinotermes lamanianus* (Sjöstedt), Renoux (1976) reported nymphal stages with antennal segments ranging from 12 to 20. The nymphs can also directly molt to the next instar, and there are seven instars altogether. Whereas nymphs of stage 1 through 3 collected from the field and brought into the laboratory were often killed by other members of the colony, the majority of the nymphs of stages 4 through 6 transformed into brachypteroid neotronics. However, the seventh instars transformed into alates even in the absence of NIF, presumably having passed the critical point in the developmental process. Noirot (1985) reported that in Rhinotermitidae, there is separation into two developmental lines, the sexual or nymphal line and the worker line, after the second molt identified by the presence or absence of wing buds. Working with young colonies of *C. formosanus*, and using the criteria of antennal segments and head width, King (1971) determined six "larval" instars. Higa (1981) reported eight growth stages having 9–16 antennal segments in workers of *C. formosanus*. In *C. lacteus*, Roisin and Lenz (1999) reported six instars followed by the alates. They further stated that the apterous line included 8–11 instars and that soldiers seemed to derive exclusively from older female workers.

This is the first study of the formation and transformation of nymphs in termites. What we have reported for *C. formosanus* may not hold true for other termites, including those from the same family or even the same genus. Further work will be required to determine what specific chemical, environmental, or nutritional factors lead to development of nymphs in this and other termite species.

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